

Comparative anatomy of five species of *Saccostrea* Dollfus and Dautzenberg, 1920 (Bivalvia: Ostreidae) from the Pacific Ocean

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ABSTRACT

Ostreids are well known for their high intraspecific variation, which makes identification problematic. The present paper provides a morpho-anatomical analysis of five species of *Saccostrea*, as well as of selected congeneric species from relevant areas in the Pacific Ocean. *Saccostrea cucullata* occurs in Africa, Indian Ocean, Arabian Sea, Red Sea, and part of the Pacific, where it lives attached to rocks and mangroves roots. *Saccostrea glomerata* occurs in the Pacific, New Zealand, Australia and the Philippines, always associated with rocks. *Saccostrea echinata* occurs from East Africa to Japan. *S. palmula* occurs from Pacific Mexico to Peru. *Saccostrea mordax* occurs in the Red Sea and the Pacific. The wide distribution and plasticity of these often sympatric species led to confusion regarding their identity. Herein we describe anatomical differences that allow for a more precise identification, especially when compared to sympatric taxa.

Additional Keywords: oyster, morphology, systematics, phenotypic plasticity

INTRODUCTION

Species of the genus *Saccostrea* Dollfus and Dautzenberg, 1920 are oysters that live on rocky shores of the Indo-Pacific region. The taxonomy of this genus is unclear, and their morphological plasticity makes identification problematic (Lam and Morton, 2006). They have small to medium-sized shells, and a left valve with a prominent ligament area, with projections in zigzag continuous and regular. The right valve is flat, bearing projections along its margin, with corresponding concavities on the left valve. The genus includes nine species (Huber, 2010): *Saccostrea cucullata* (Born, 1778) – the type species; *Saccostrea cirumsuta* (Gould, 1850); *Saccostrea echinata* (Quoy and Gaimard, 1835); *Saccostrea glomerata* (Gould, 1850); *Saccostrea kegaki* Torigoe and Inaba, 1981; *Saccostrea malabonensis* (Faustino, 1932); *Saccostrea*

palmula (Carpenter, 1857); *Saccostrea scyphophilla* (Peron and Lesueur, 1807) and *Saccostrea spatulata* (Lamarck, 1819).

Because of shell plasticity, the taxonomy of *Saccostrea* has been a troublesome matter; e.g., some “forms” of *S. cucullata* have been assigned different names by different authors, i.e., *S. echinata*, *S. mordax*, *S. glomerata* (Lam and Morton, 2004). Molecular studies (e.g., Lam and Morton, 2004; 2006; 2009; Wang and Guo, 2008a; 2008b) have been conducted in attempts to resolve this taxonomic confusion and better understand the generic distribution. Reports on the difficulty of proper species identification, caused by the wide variation in body size and coloration, are frequent in the literature and determine a baffling scenario (Awati and Rai, 1931). This problem was further confirmed by Lam and Morton (2006: 1): “The geographical distribution of lineages of *Saccostrea* is somewhat uncertain because of taxonomic confusion”. Moreover, the widespread, sometimes overlapping, distributions of these species also make identification problematic (Huber, 2010).

Molecular systematic studies of *Saccostrea* are few and constrained by many taxonomical issues (Lam and Morton, 2006). Furthermore, the genus has been reported to display ecomorphological variation (Tack et al., 1992). For instance, these facts may help explain why all *Saccostrea* species from Thailand were previously assumed to be a single species, *S. cucullata* (Visoothiviseth et al., 1998). However, the results of Klinbunga et al. (2005) indicated that more than one species of *Saccostrea* may be present in Thai waters, which may have implications regarding its commercial use.

In this paper, we perform a detailed morpho-anatomical study of five *Saccostrea* species from the Pacific Ocean: *S. cucullata*, from Africa, the Indian and Arabian Oceans, the Red Sea and part of the Pacific Ocean; *S. glomerata*, from the Pacific, New Zealand, Australia and the Philippines; *S. echinata*, from East

Africa and Japan; *S. palmula* from Mexico to Peru, in the Pacific and *S. mordax*, from the Red Sea and the Pacific Ocean.

MATERIALS AND METHODS

The study material was preserved in 70–99% ethanol. Specimens were immersed in the preservative fluid and dissected by standard techniques under a stereomicroscope (Simone, 1997; 2009; 2011). Details of all systems (mantle cavity, mantle edge, muscles, digestive, circulatory, excretory, and nervous systems) and organs were examined. Drawings were done with the aid of a *camera lucida*.

The studied samples are held at several institutional collections: National Museum of Natural History, Smithsonian Institution (USNM), Florida Museum of Natural History (UF), Field Museum of Natural History (FMNH), and Museu de Zoologia da Universidade de São Paulo (MZSP).

The following abbreviations are used in the figures: accessory heart (**ah**), adductor muscle (**am**), anus (**an**), auricles (**au**), chomata (**ch**), dorsal hood (**dh**), esophagus (**oe**), external fold (**ef**), gastric shield (**gs**), gills (**gi**), heart (**he**), hood (**ho**), inner fold (**if**), intestine (**in**), mantle edge (**me**), middle fold (**mf**), muscle scar (**im**), pallial muscles (**pm**), palps (**pa**), Quenstedt muscle (**qm**), rectum (**rt**), sorting area (**sa**), typhlosole (**ty**), umbonal cavity (**uc**), undulations (**pl**), ventricle (**ve**), visceral ganglia (**vg**), visceral mass (**vm**).

SYSTEMATICS

Genus *Saccostrea* Dollfus and Dautzenberg, 1920

Type Species: *Ostrea saccellus* Dujardin, 1835 (= *O. cucullata* Born, 1778)

Diagnosis: Shell cup-shaped, with marginal denticles, promial chamber on the right side.

Distribution: This genus is restricted to tropical and sub-tropical waters from eastern Atlantic, Indo-West Pacific, and eastern Pacific, while it is absent in the western Atlantic; in saline areas (open ocean), but occasionally occurring in mangrove areas. Most species live exposed, fixed on rocks or coral (Harry, 1985).

Saccostrea cucullata (Born, 1778)

(Figures 1–15)

Ostrea cucullata [sic] Born, 1778: 100.

Ostrea cucullata Born, 1780: 114, pl. 6, figs 11, 12; Dillwyn, 1817: 277; Smith, 1890: 322; Awati and Rai, 1931: 1–107.

Ostrea cornucopiae Gmelin, 1791: 3336; Küster, 1868: 77.

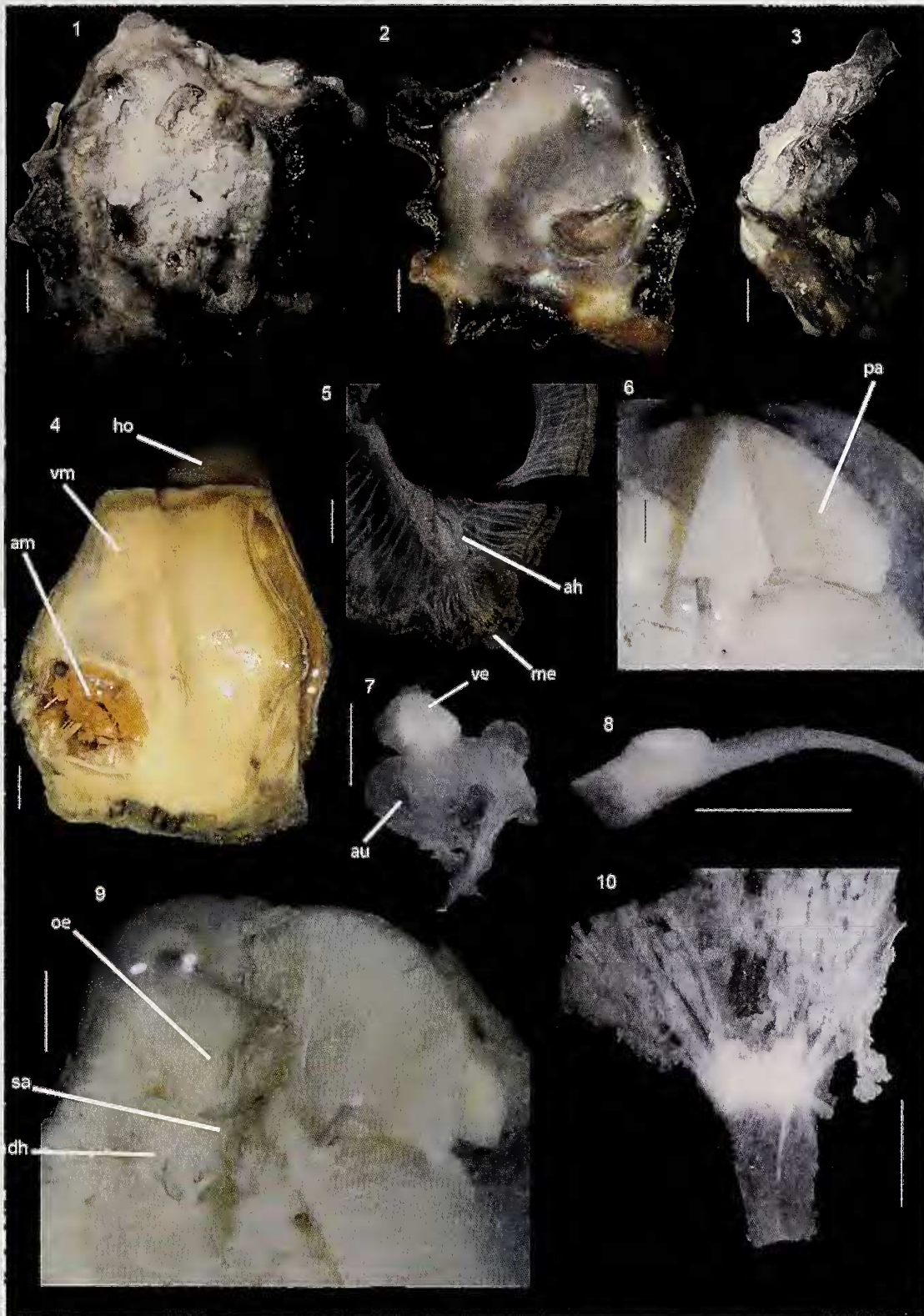
Lophia cornucopiae: Röding, 1798: 169.

Ostrea gibbosa Lamareck, 1819: 209; Hanley, 1856: 301.

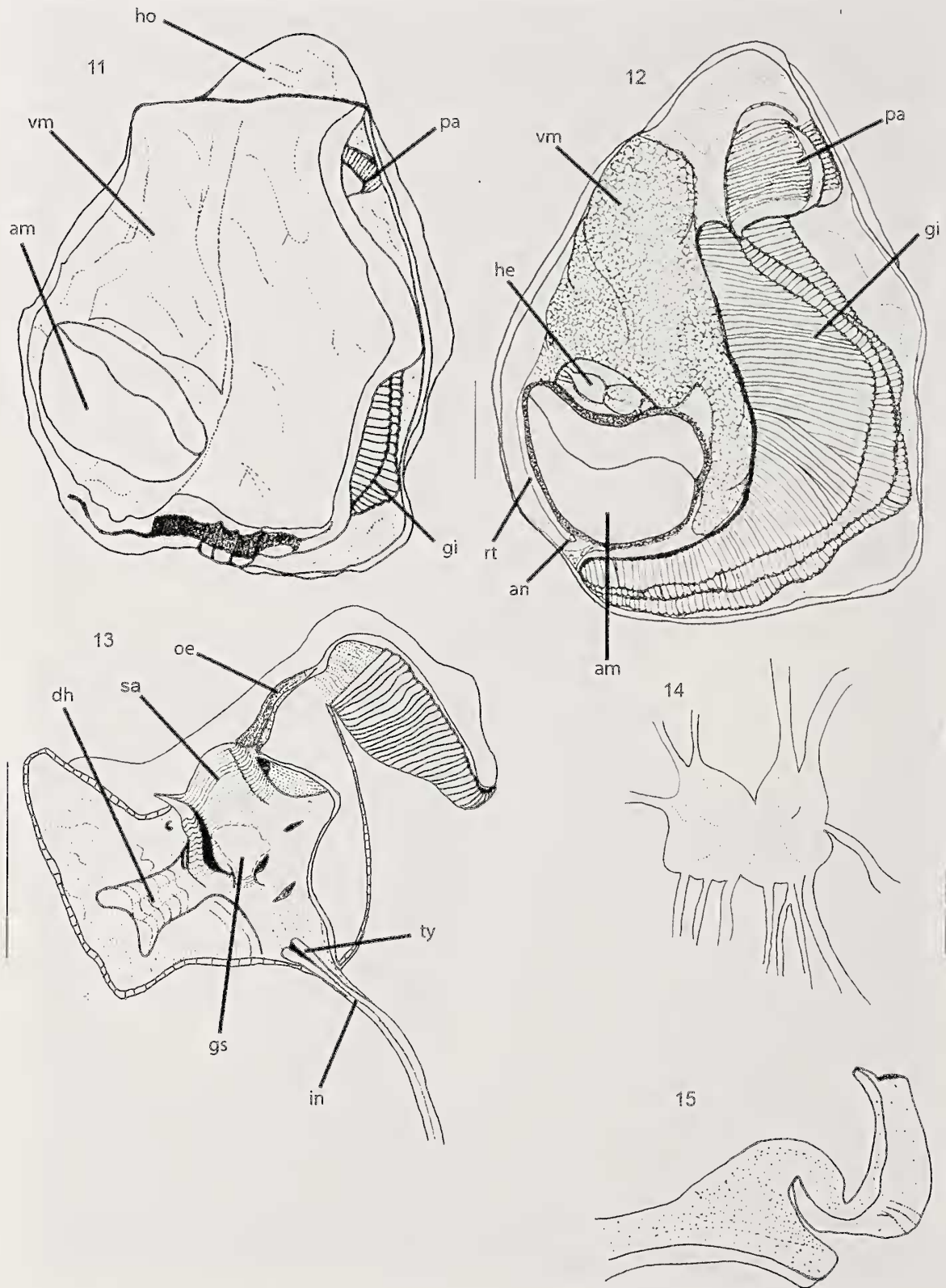
Crassostrea cucullata Ranson, 1960: 20.

Saccostrea cucullata: Stenzel, 1971: N1134–N1135, fig. J106; Morris, 1985: 125–128, Pl. 3, figs E–G; Lam and Morton, 2003: 110–112, pls. 11, 12; Lam and Morton, 2009: 482, fig. 1: 483.

Description: SHELL: Elongated, generally cup-shaped, to 100 mm. Right (upper) valve flat or slightly convex (Figure 2). Ligament alivincular. Left valve fixed to substrate, cupped and larger than right valve. Umbonal cavity of left valve. Margins of both valves with angles sculpture in the edge (Figures 1, 3); inner edge of right valve with small elongated denticles (Figure 2) producing corresponding depressions on left valve. Adductor muscle scar reniform, occupying ¼ of total shell height, in posterodorsal region (Figure 2), striate, white or grayish. Outside of valves variable from white to gray, light or dark brown, green or purple. Inner surface white, with occasional purple spots. ADDUCTOR MUSCLE: Reniform or slightly oval, located in posterior region, occupying ¼ of total soft part height (Figures 4, 11, 12). MANTLE: Mantle lobes thick, with well-defined pallial muscles, most abundant near adductor muscle (Figures 4, 5). Hood formed by junction of anterior mantle lobes. Hood robust and well-defined, usually free or filled by gonad mass (Figures 4, 11). MANTLE EDGE: Pleated and thick, dark, yellow with brown spots, bearing three similar-sized folds. Middle and inner folds with finger-like, uniformly distributed papillae, single or in pairs, with variable length (Figure 5). GILLS: Gills occupying 50% of total height. Demibranchs moderately thick, ~1/3 as thick as gill fold (Figures 6, 12). CIRCULATORY SYSTEM: Ventricle large, thick-walled, with internal beams crossing each other in various directions; opaque white. Outer part of auricles thin, translucent, trabecular; external portion of auricles bearing small, saculiform structures (Figure 7). Pair of kidneys triangular, tubular, mottled by light brown marks. Each kidney having direct communication with pericardium and gonad on medial side and communicating laterally by short chamber. Renal opening located on opposite side of cerebro-visceral connective. DIGESTIVE SYSTEM: Palps large, length ¼ of gill size, spatuliform; internal surface with pleats extending transversely to edge (Figure 6). Stomach in globular region of visceral mass, typically occupying ¼ of total length. Esophagus short, ½ of palp length, (Figure 13). Sorting area of stomach (sa) short (1/2 of palp length) and wide with typhlosole beginning in posterior region of stomach (Figure 9, 13). Intestine separated from style sac, returning in opposite direction, passing usually behind pericardium, immersed in gonads; narrowest portion of intestine surrounding adductor muscle. Rectum long and thin, surrounding adductor muscle almost until canopy-gill junction. Anus sessile, rounded, ½ of height of adductor muscle, with single fold. REPRODUCTIVE SYSTEM: Gonad composed of two lobes of follicular aspect, occupying ¼ of total animal size. Dorsally and ventrally spread in left lobe and right lobe; shape indistinct from each other. Two pairs of separate systems of genital channels, same as described above (excretory system). NERVOUS SYSTEM: Nervous system similar to other ostreid species. Pair of



Figures 1–10. *Saccostrea cucullata*, shell and anatomical features. **1.** Shell in right view. **2.** Right valve, internal view. **3.** Shell in ventral view. **4.** Complete soft parts; (ho) hood; (vm) visceral mass; (am) adductor muscle. **5.** Dissected mantle lobe, mantle edge and accessory heart; (ah) accessory heart; (me) mantle edge. **6.** Palps (pa), right-slightly ventral view, outer right hemipalp deflected. **7.** Heart isolated, showing ventricle (ve) and auricles (au). **8.** Anus and rectum. **9.** Anterior region, right view, digestive system exposed; (oe) esophagus; (sa) selection area; (dh) dorsal hood. **10.** Visceral ganglia, ventral view, adjacent layer of tissues also shown. Scale bars = 1 cm.



Figures 11–15. *Saccostrea cucullata*, anatomical features. **11.** General view of soft parts; (ho) hood; (vm) visceral mass; (pa) palps; (am) adductor muscle; (gi) gills. **12.** General view, right mantle lobe removed; (vm) visceral mass; (pa) palps; (am) adductor muscle; (gi) gills; (he) heart; (rt) rectum; (an) anus. **13.** Stomach, right view, opened longitudinally; (oe) esophagus, (sa) selection area, (dh) dorsal hood, (gs) gastric shield, (ty) typhlosole, (in) intestine. **14.** Visceral ganglia, ventral view. **15.** Detail of anus. Scale bars = 1 cm.

cerebral ganglia in anterior region, near palps; link at pair of visceral ganglia by connectives; visceral ganglia occupying 1/15 of adductor muscle area, with two pairs of branches in anterior region, three in posterior region and one laterally (Figures 10,14).

Type Material: Born's holotype is located at the Naturhistorisches Museum Vienna (Morris, 1985). *Ostrea cornucopiae*, Syntypes, Genève Museum n° 1089141, Lamarek Coll. (examined).

Material Examined: **CHINA:** Hong Kong, North Pacific Ocean, USNM 858434, 3 specimens; **NEW ZEALAND:** South Pacific Ocean, USNM 886486, 5 specimens; **THAILAND:** Chantaburi, Kung Kraben Bay, MZUSP 55270, (L. R. Simone coll. 24/vii/2005), 6 specimens.

Distribution: Indo-West Pacific.

***Saccostrea glomerata* (Gould, 1850)**
(Figures 16–27)

Ostrea glomerata Gould, 1850: 346; 1852: 462; Sowerby, 1871: sp. 64.

Ostrea attenuata Sowerby, 1871: pl. 21.

Ostrea vitrefacta Sowerby, 1871: sp. 80; Lamy, 1929: 166; Île-Rodriguez, 1938: 289.

Ostrea mordax.—Hutton, 1873b: 84 (*non* Gould, 1850).

Lopha glomerata.—Finlay, 1928: 268.

Ostrea forskali var. *glomerata*.—Lamy, 1929: 158.

Ostrea (Lopha) glomerata.—Hiro, 1936: 36; Wada, 1942: 70.

Crassostrea cucullata.—Ranson, 1967: 188; Nishimura et al., 1998: 85 (*non* Born, 1778).

Saccostrea glomerata.—Torigoe, 1981: 310, 332; Dinamani, 1991a: 335; Xu, 1997: 94.

Saccostrea cucullata.—Oliver, 1992: 88; Nishimura et al. 1998: 86, 88 (*non* Born, 1778).

Description: SHELL: Rounded, to 50 mm; left valve concave, slightly larger than right valve, lacking well-developed umbonal cavity (Figure 16). Right valve slightly convex; ligament short, with mild bulging in central region (Figure 17); margins of both valves with well-developed angles (Figures 16, 17); color internally dark brown at edges, fading toward median region of shell. Right valve with single row of rounded denticles spread along entire edge (Figure 17), with corresponding depressions on left valve. Adductor muscle scar reniform, occupying 1/5 of total inner shell area, located in median region, with anterior portion normally pigmented gray/brown and posterior portion with pigmented lines; surface slightly pearlescent, white-colored. Quenstedt muscle scar rounded, occupying 1/20 of total area of adductor muscle scar, located in anterior-ventral region of valves (Figure 17). MUSCLES: Adductor muscle reniform, occupying 1/3 of total height, with a convexity in posterior region (Figures 18, 24). MANTLE: Mantle lobes slightly thick, with well-defined pallial muscles more abundant near adductor muscle (Figures 18, 19). Mantle edge thick, reddish; middle fold with 3–4 short to long, elongated papillae; internal fold with

short to medium papillae, presenting 2–3 medium papillae for each short one (Figure 19). GILLS: Gills occupying 1/2 total body size. Alimentary channel narrow, ~1/5 as thick as gill fold (Figure 18). HEART: Heart well-developed. Ventricle relatively large, with internal bundles crossing each other in different directions, light beige. Auricles thin, with more abundant bundles, same texture, and coloration, but more elongated than ventricle (Figure 21). DIGESTIVE SYSTEM: Palps occupying ~1/5 of visceral mass, spatuliform, rounded; internal surface with plicae extending transversely to edge (Figures 20, 23, 25). Esophagus long and narrow; length ~1/2 of palp length (Figures 22, 26). Selection area (sa) long and thin, with typhlosoles beginning in posterior region of stomach (Figures 22, 26). Intestine passing behind pericardium, with narrowest portion surrounding adductor muscle. Rectum slightly long and thin, contouring adductor muscle at dorsomedial region. Anus with single fold (Figure 22). NERVOUS SYSTEM: Two pairs of branches in the anterior region and three in posterior region (Figure 27).

Type Material: Holotype, USNM 5960 (examined); Paratypes USNM 612314, MCZC 178590, 178591.

Material Examined: **Fiji:** Nanuya-Lailai Island, Yasawa Group T. Moala. MZUSP 71454; 2 specimens.

Distribution: India to Australia and New Zealand.

***Saccostrea echinata* (Quoy and Gaimard, 1835)**
(Figures 28–42)

Ostrea mytiloides Lamarck, 1819: 207; Deshayes, 1836: 227; Hanley, 1856: 300; Hidalgo, 1905: 387; Lamy, 1924: 155, 1929: 138 (*non* Gmelin, 1791).

Ostrea echinata Quoy and Gaimard, 1835: 455; Hanley, 1856: 302; Küster, 1868: 76; Hidalgo, 1905: 387; Chen et al. 1980: 174.

Ostrea arakanensis Sowerby, 1871: sp. 83.

Ostrea nigromarginata Sowerby, 1871: sp. 85; Lamy, 1928: 140.

Ostrea cucullata.—Pilsbry, 1895: 146 (*non* Born, 1778).

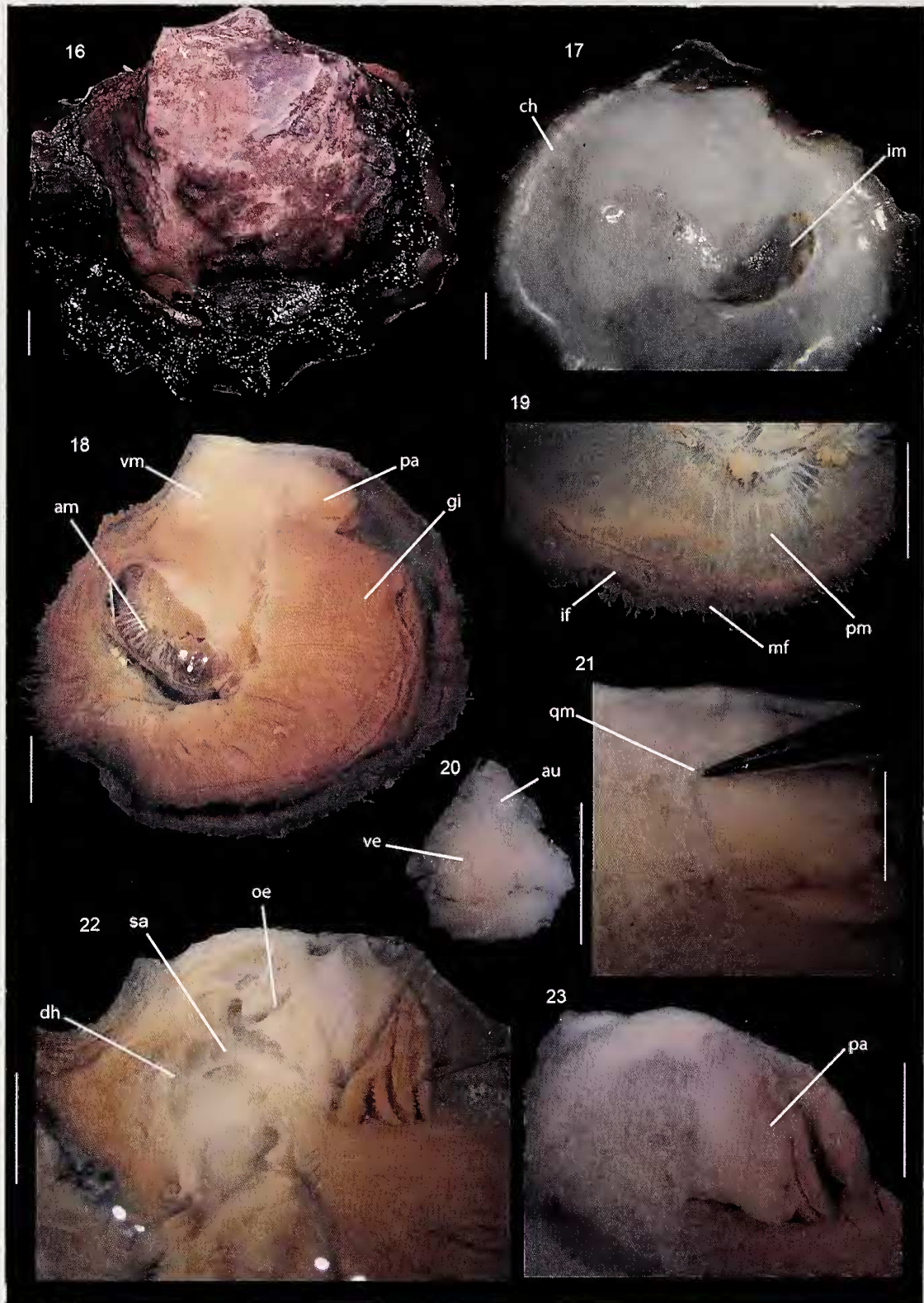
Crassostrea echinata.—Thompson, 1954: 152; Carreon, 1969: 113.

Saxostrea mytiloides [sic].—Habe and Kosuge, 1966: 145 (*non* Gmelin).

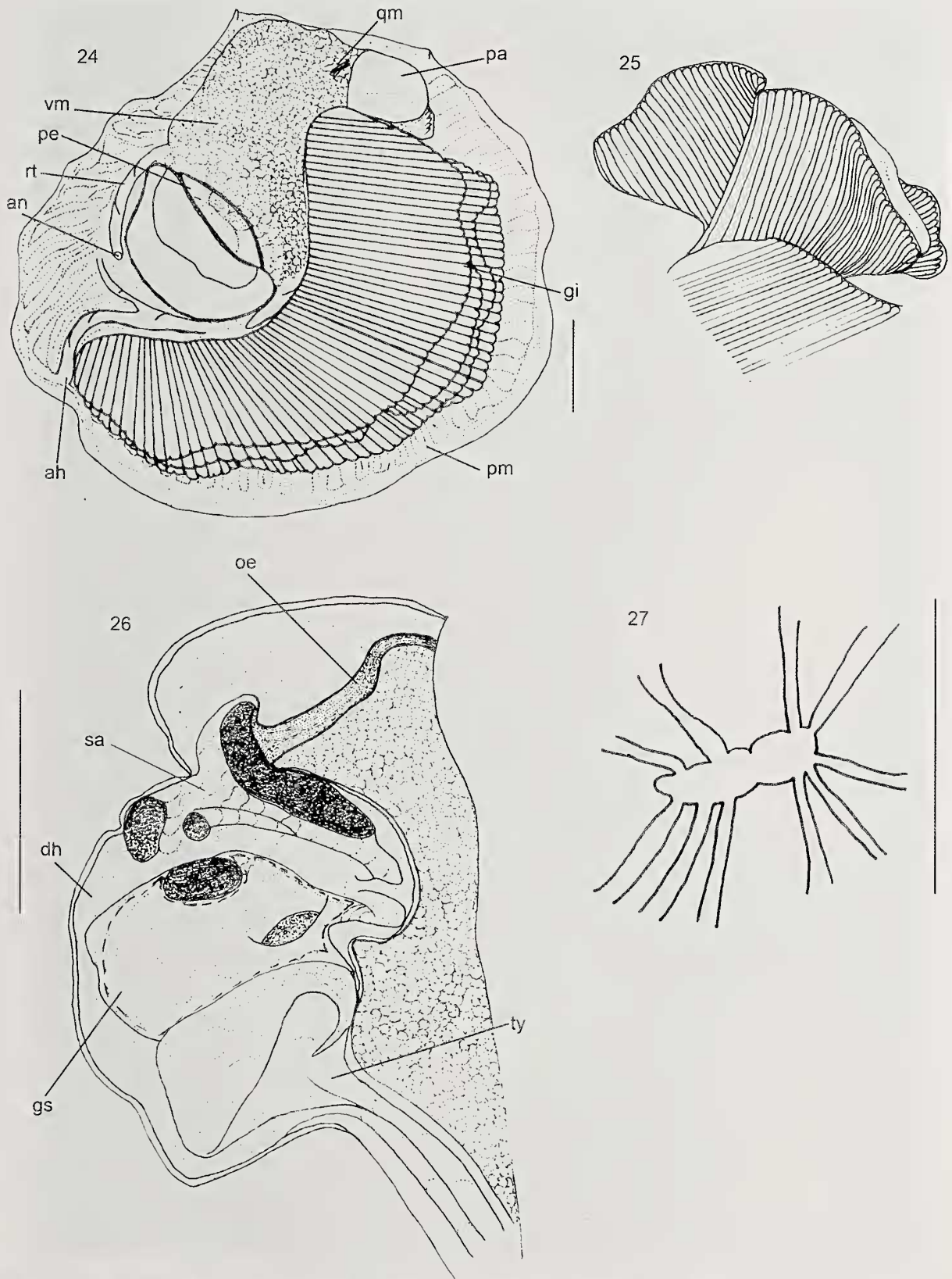
Saccostrea echinata.—Stenzel, 1971: N962; Torigoe and Inaba, 1981: 126; Torigoe, 1981: 308, 330; Li and Qi, 1994: 171; Hayami, 2000: 927.

Saccostrea cucullata.—Morris, 1985: 125; Harry, 1985: 150; Oliver, 1992: 88, 91; Xu, 1997: 95 (*non* Born, 1778).

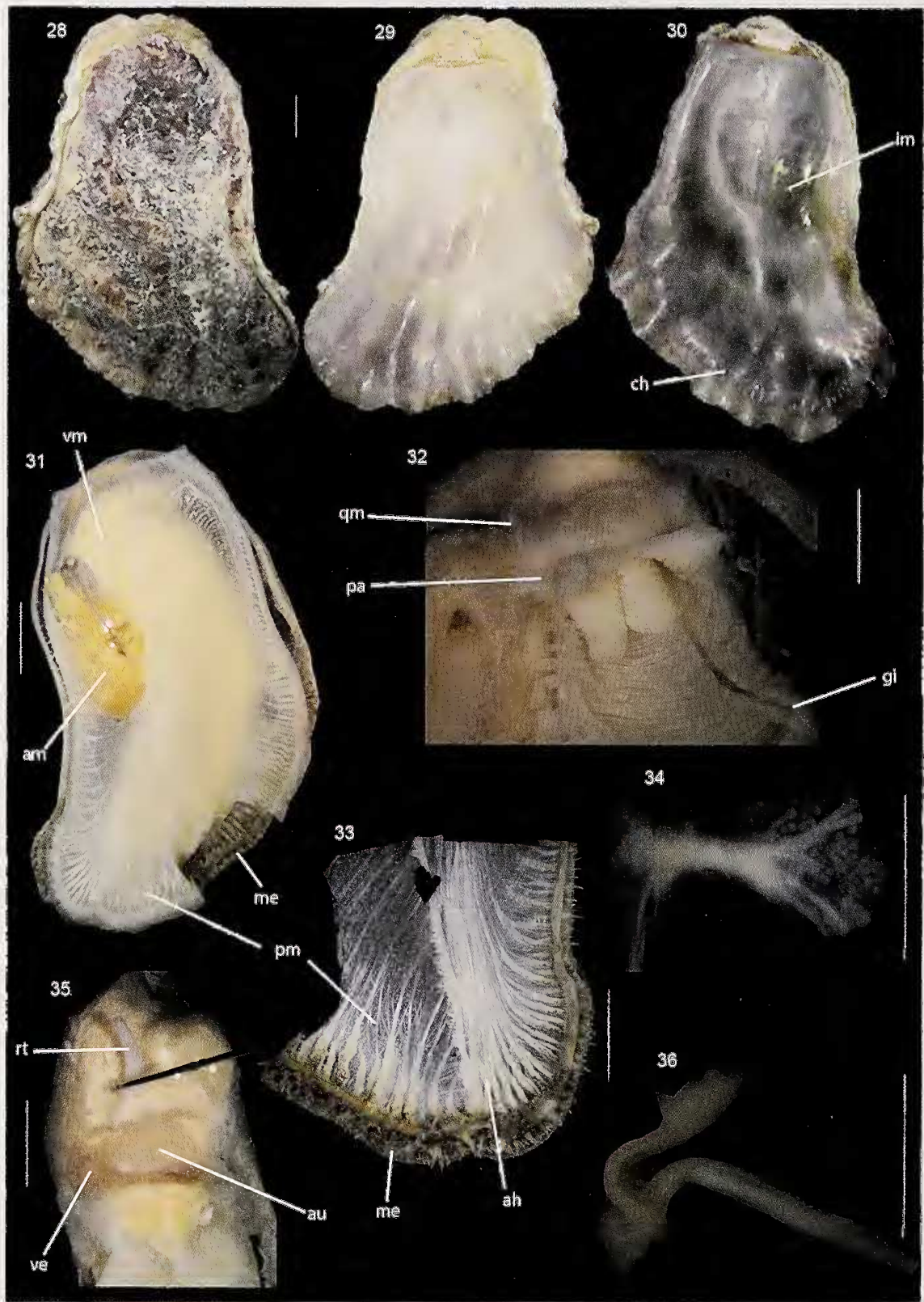
Description: SHELL: Elongated, ~ 60 mm, with slight ripples in margin of valves extending toward central region (Figures 28–30); left valve slightly larger than right valve, with deep umbonal cavity, lacking any major projections (Figure 29); internal color white/cream to gray. Adductor muscle scar elongate-reniform, occupying ~1/4 of total height of shell, non-pigmented (Figure 30). Denticles present across edge of right valve (Figure 30),



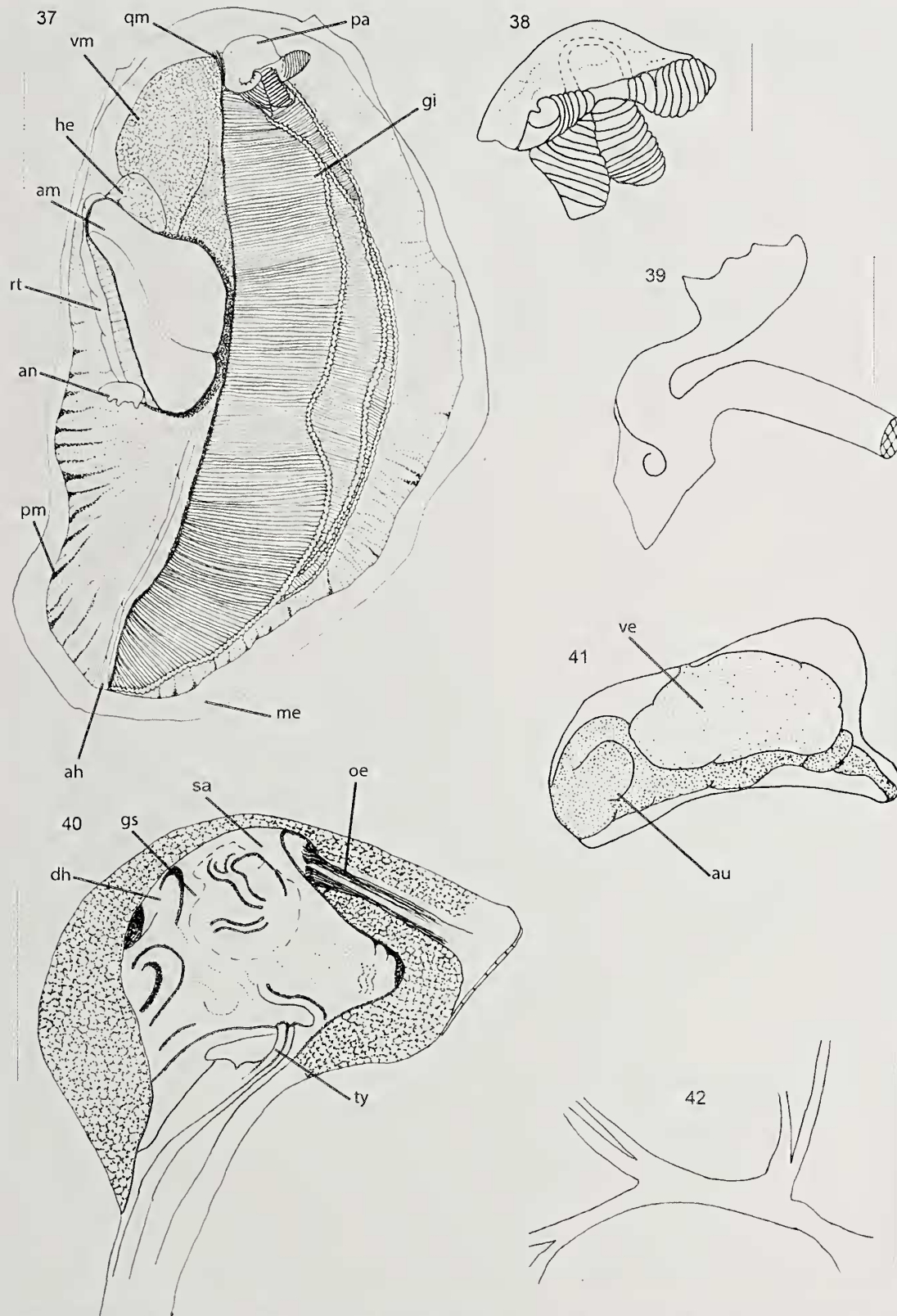
Figures 16–23. *Saccostrea glomerata*, shell and anatomical features. **16.** General right view. **17.** Right valve, internal view; (ch) chomata, (im) muscle impression. **18.** General view of soft parts right view, right mantle lobe removed; (vm) visceral mass, (am) adductor muscle, (pa) palps, (gi) gills. **19.** Mantle lobes and edge; (if) inner fold; (mf) middle fold; (pm) pallial muscles. **20.** Heart, ventral view; (ve) ventricle; (au) auricle. **21.** Anterior region, (qm) Quenstedt muscle. **22.** Anterior region, right view, with Stomach opened longitudinally; (oe) esophagus, (sa) selection area, (dh) dorsal hood. **23.** Palps (pa), right-slightly ventral view. Scale bars = 1 cm.



Figures 24–27. *Saccostrea glomerata*, anatomical features. **24.** General right view of soft parts; (qm) Quenstedt muscle, (pa) palps, (gi) gills, (pm) pallial muscles, (ah) accessory heart, (an) anus, (rt) rectum, (pe) pericardium, (vm) visceral mass. **25.** Detail of palps. **26.** Stomach opened longitudinally, right view; (oe) esophagus, (sa) selection area, (dh) dorsal hood, (ty) typhlosole. **27.** Visceral ganglia. Scale bars = 1 cm.



Figures 28–36. *Saccostrea echinata*, shell and anatomical features. 28. External view. 29. Internal view, left valve; (im) muscle impression; (ch) chomata. 30. Internal view right valve. 31. General view of soft part; (vm) visceral mass, (am) adductor muscle, (me) mantle edge. 32. Anterior region; (qm) Quenstedt muscle, (pa) palps, (gi) gills. 33. Mantle edge (me), detail of pallial muscles (pm) and accessory heart (ah). 34. Visceral ganglia. 35. Heart, (ve) ventricle, (au) auricle and rectum (rt). 36. Anus with expansion and rectum. Scale bars = 1 cm.



Figures 37–42. *Saccostrea echinata*, anatomical features. **37.** General view of soft parts; (qm) Quenstedt muscle, (vm) visceral mass, (he) herart), (am) adductor muscle, (rt) rectum, (an) anus, (pm) pallial muscles, (ah) accessory heart, (me) mantle edge, (gi) gills, (pa) palps. **38.** Palps, detail of median fusion of external hemipalps. **39.** Anus (an) and rectum (rt), detail of expansion in anus. **40.** Stomach, right view; (oe) esophagus, (sa) selection area, (gs) gastric shield, (dh) dorsal hood, (ty) typhlosole. **41.** Heart in pericardium; (ve) ventricle, (au) auricle. **42.** Visceral ganglia. Scale bars = 1 cm.

with corresponding depressions on left valve (Figure 29), distributed in various rows along posterior region, being elongated, rounded or both. **MUSCLES:** Reniform, occupying $\sim 1/4$ of total height, with a convexity in posterior region (Figures 30, 37). **MANTLE:** Mantle edges delicate, with well-defined pallial muscles in all mantle surfaces. Hood filled with gonads (Figures 31, 33, 37). **MANTLE EDGE:** Mantle edge thick, with yellow and/or brown pigmentation. Papillae of middle fold alternately long and short; usually with a long papilla for each three short ones. Accessory heart with only one branch on both lobes, thin and translucent; lobes not reaching adductor muscle (Figure 33). **GILLS:** Gills occupying $1/2$ of total height. Alimentary chamber thick, $\sim 1/2$ as thick as gill fold (Figures 32, 37). **CIRCULATORY SYSTEM:** Ventricle thin, usually translucent, auricles elongated, less cross-linked, non-pigmented (Figures 35, 41). **DIGESTIVE SYSTEM:** Palps small, $\sim 1/4$ of adductor muscle size, curved, sickle-shaped, with folds along anterior margin. External palps fused in middle region and overlying internal palps (Figures 32, 39). Esophagus long ($\sim 1/3$ of adductor muscle) and thin. Selection area of stomach (sa) short ($\sim 1/2$ of esophagus size) and wide, with typhlosole (ty) beginning in posterior region of stomach (Figure 38). Intestine passing behind pericardium; narrowest portion circling adductor muscle. Rectum long and thin, girdling adductor muscle. Anus papillae shaped similarly to shell (Figure 35, 36, 40). **NERVOUS SYSTEM:** With three branches in anterior region and only one in posterior region (Figures 34, 42).

Type Material: Holotype in MNHN (examined).

Material Examined: MARIANA ISLANDS: Guam, UF 284793; 3 specimens.

Distribution: E. Africa to Japan.

***Saccostrea palmula* (Carpenter, 1857)**
(Figures 43–53)

Ostrea palmula Carpenter, 1857b: 163, 550; 1864: 538; Dall, 1914: 2; Lamy, 1929: 150; Keen, 1971: 84; Abbott, 1974: 456.

Ostrea plumula [sic].—Carpenter, 1857b: 351, 353.

Ostrea amara Carpenter 1864a: 363; 1864: 541, 552, 621, 666; Lamy, 1930: 242.

Ostrea frons.—Carpenter, 1864: 520 (*non* Linnaeus, 1758).

Ostrea mexicana Sowerby, 1871: sp. 35.

Ostrea cumingiana var. *Mexicana*.—Dall, 1914: 2.

Ostrea conchaphila (pars).—Abbott, 1974: 456 (*non* Carpenter, 1857).

Saccostrea palmula.—Harry, 1985: 138.

Crassostrea palmula.—Rodríguez and García-Cubas, 1986: 269.

Description: **SHELL:** Shell rounded, to ~ 60 mm. Left valve larger than right valve, with small umbonal cavity and slight projection in ligament region; projections and evident ripples present along margin (Figures 43, 44). Right valve smaller than left valve, opercular, following

pattern of expansion of left valve (Figure 44). Color white/cream with purple spots on outer surface; inner surface white, slightly nacreous, with occasional purple spots and lines. Adductor muscle scar well-defined, showing purple concentric lines in anteroventral portion of valves, reniform (Figures 44, 45), occupying $1/5$ of total height. Denticles rounded in anterior region, aligned, uniformly distributed; corresponding depressions on right valve shallow, almost inconspicuous (Figure 44). **MUSCLES:** Same morphology as other species, reniform (Figures 46, 47, 50), occupying $\sim 1/5$ of total height. **MANTLE:** Mantle lobes thin, with well-defined pallial muscles in posterior region (Figures 46, 50); hood absent. Mantle edge thinner, beige to cream; middle fold bearing two to five finger-like, medium papillae for each two long ones (Figure 47). Accessory heart with three well-defined branches, reaching and circling adductor muscle in ventral region (Figure 47). **GILLS:** Gills occupying $\sim 1/3$ of total body size. Alimentary chamber narrow (Figures 46, 48). **HEART:** Ventricle elongated, slightly thick, reticulated and whitish. Auricles thin, small and non-pigmented (Figures 46, 50). **DIGESTIVE SYSTEM:** Palps large, occupying half as large as adductor muscle, thin, with folds on upper margin (Figures 48, 51).

Nervous System: Visceral ganglia with two anterior expansions, two lateral and two posterior ones (Figures 49, 53).

Type Material: Syntypes, BMNH 1857.6. 4.735, 1857.6. 4.736, 1857.6. 4.737 (examined).

Material Examined: PANAMA: Miraflores Lock, USNM 734199, 2 specimens; Arraijan, FMNH 27226, 2 specimens.

Distribution: Mexico to Peru.

***Saccostrea mordax* Gould, 1850**
(Figures 54–64)

Ostrea mordax Gould, 1850: 346; 1852: 464; 1856: pl. 43; Sowerby, 1871: sp. 31; Saville-Kent, 1891: 2; 1892: 65, 245; Hutton, 1937b: 84; Hirase and Taki, 1951: pl. 7.

Ostrea cornucopiae Saville-Kent, 1891: 3 (*non* Gmelin, 1791).

Ostrea mordax var. *cornucopiaeformis* Saville-Kent, 1893: 248.

Ostrea cucullata.—Iwakawa, 1915: 15; 1919: 254; Hatai, 1941: 58; Wells and Bryce, 1988: 162.

Ostrea forskali var. *sueli* Lamy, 1925: 192.

Ostrea (Lopha) cucullata.—Kuroda, 1928: sp. 36; Hirase, 1930: 25; 1934: 5; Takatsuki, 1949: 5 (*non* Born, 1778).

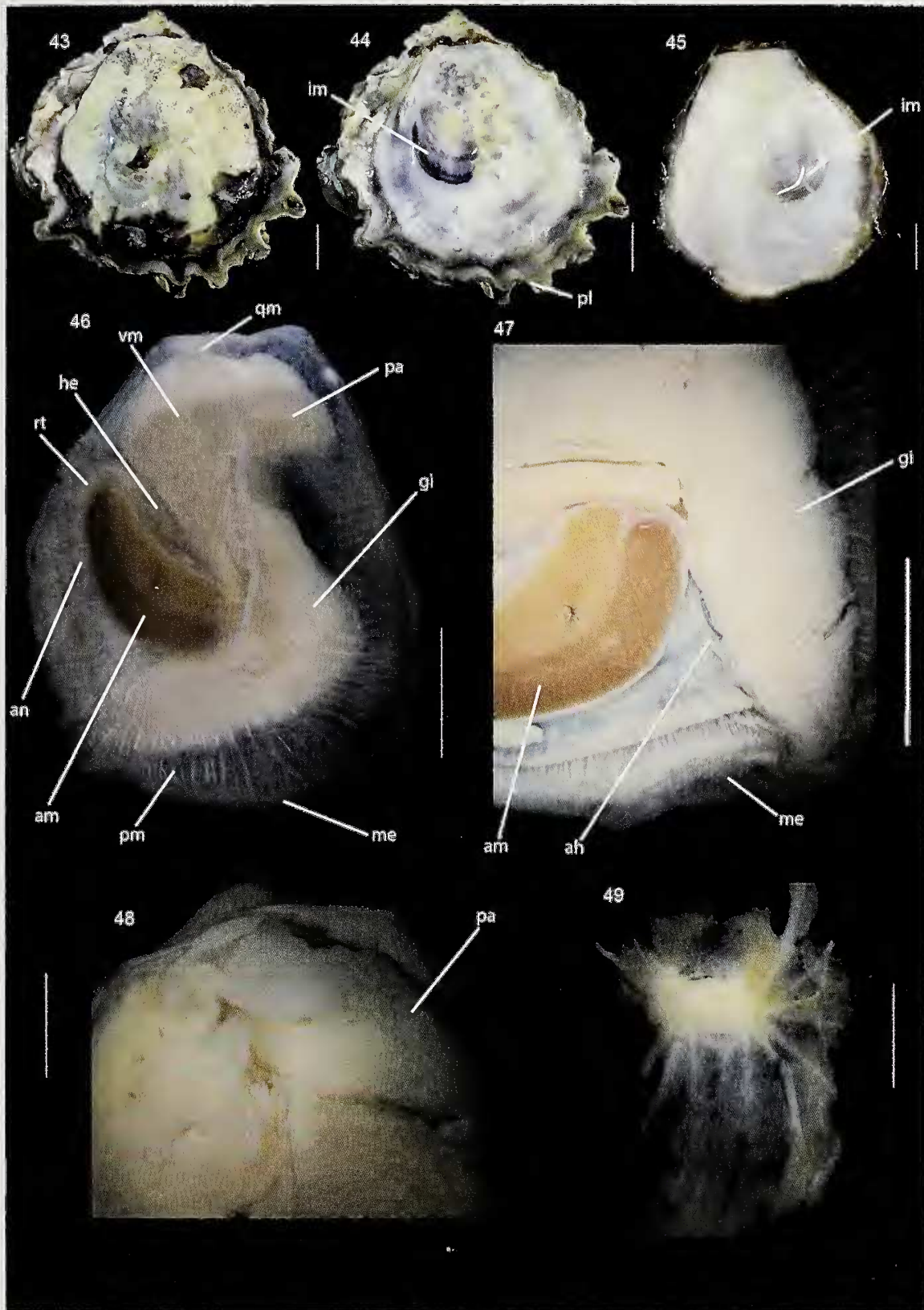
Ostrea forskali var. *mordax*.—Lamy, 1929: 158.

Ostrea (Lopha) mordax.—Kuroda, 1930: 51; Tchang and Lo, 1956: 74.

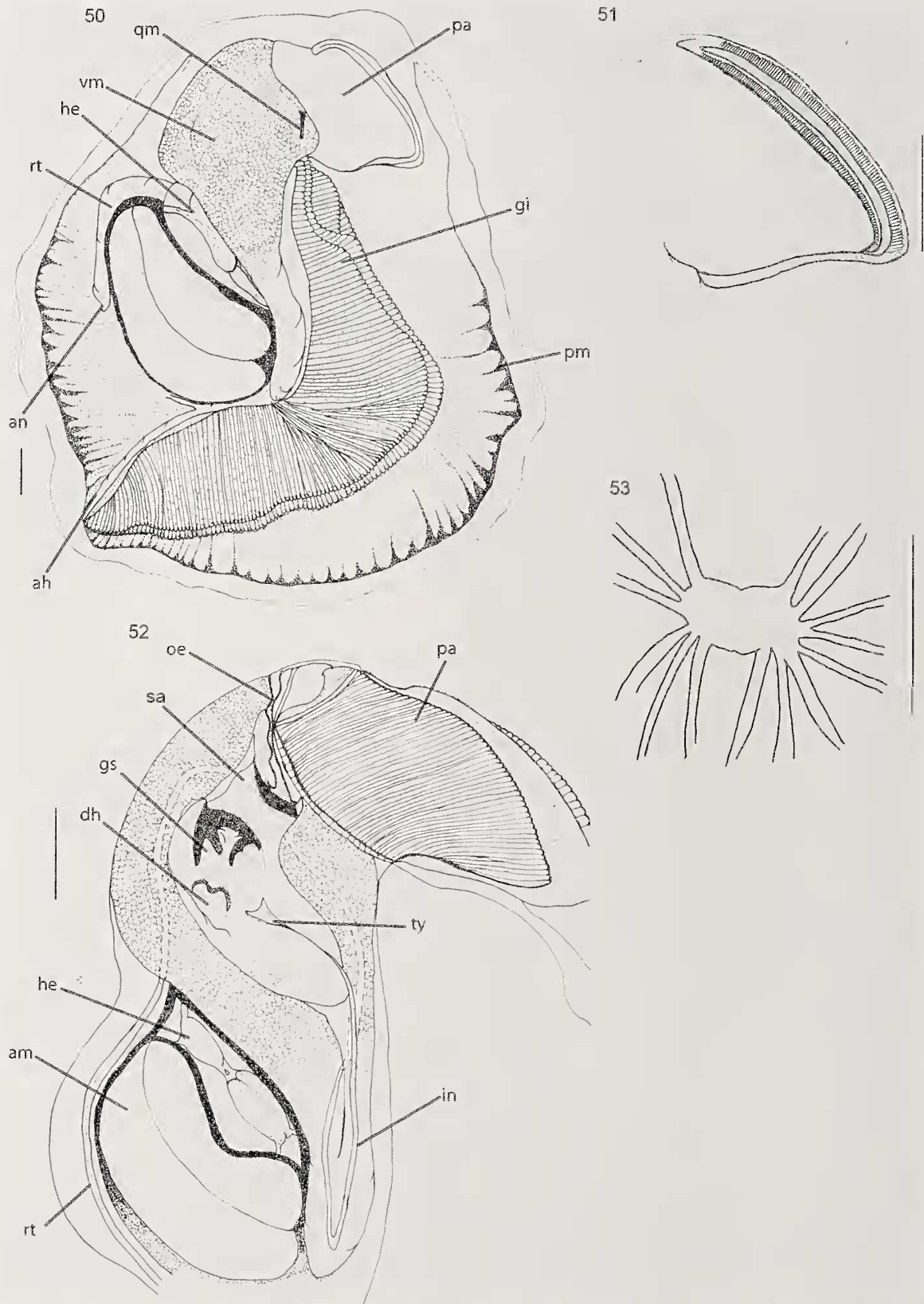
Saxostrea amasa Iredale, 1939: 399; Allan, 1959: 273.

Ostrea glomerata.—Blanco et al., 1951: 52 (*non* Gould, 1850).

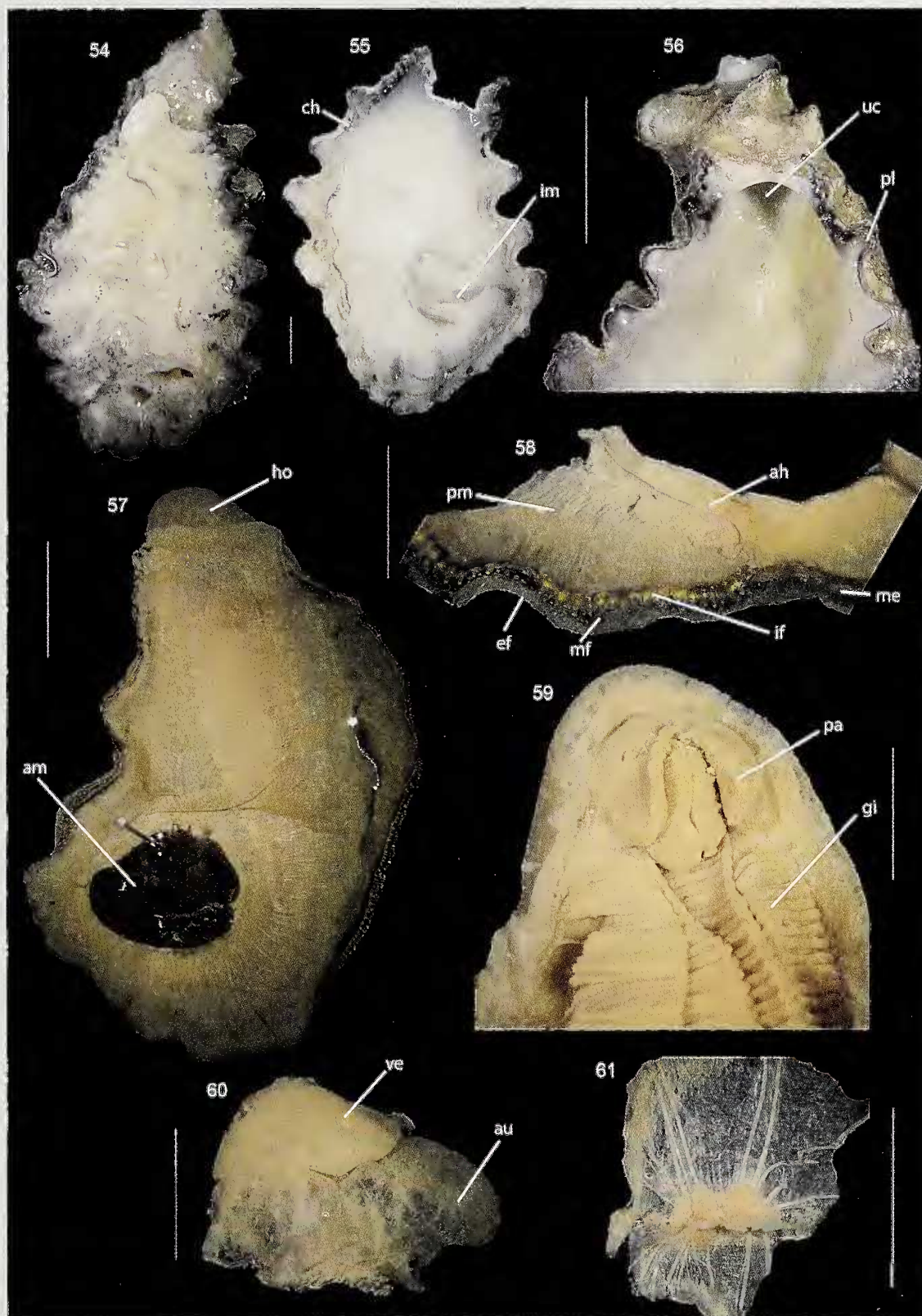
Crassostrea amasa.—Thompson, 1954: 154; Carreon, 1969: 111.



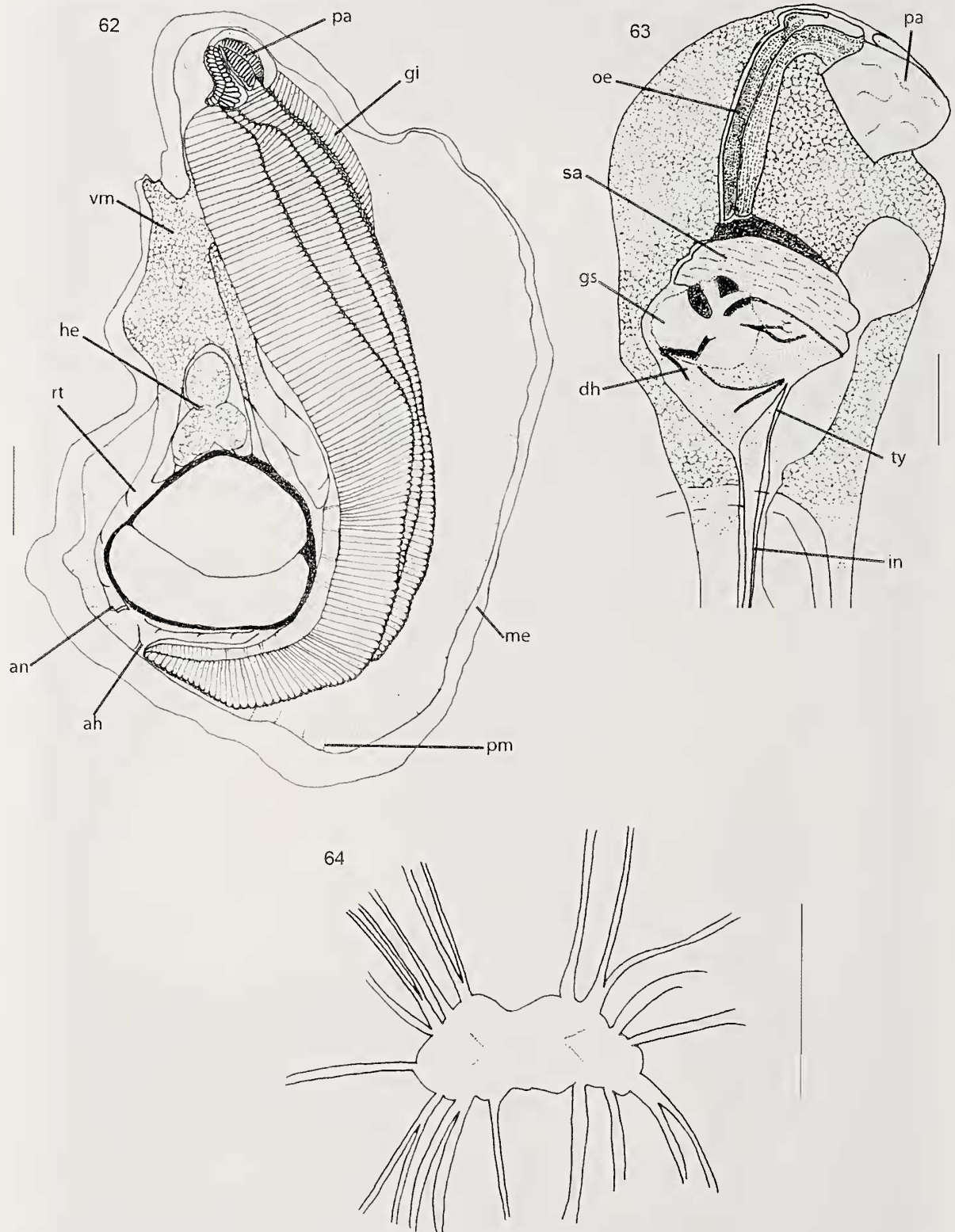
Figures 43–49. *Saccostrea palmula*, anatomical features. **43.** External view. **44.** Internal view of left valve, (im) muscle impression. **45.** Internal view of right valve. **46.** General view of soft parts; (qm) Quenstedt muscle, (vm) visceral mass, (he) heart, (rt) rectum, (an) anus, (am) adductor muscle, (pm) pallial muscles, (me) mantle edge, (gi) gills, (pa) palps. **47.** Posterior region, detail for a gills (gi), mantle edge (me), accessory heart (ah) and adductor muscle (am). **48.** Detail of palps. **49.** Visceral ganglia. Scale bars = 1 cm.



Figures 50–53. *Saccostrea palmula*, shell and anatomical features. **50.** General view of soft parts; (qm) Quenstedt muscle, (vm) visceral mass, (he) heart, (rt) rectum, (an) anus, (ah) accessory heart, (pm) pallial muscles, (gi) gills, (pa) palps. **51.** Detail of palps. **52.** Stomach, right view; (oe) esophagus, (sa) selection area, (gs) gastric shield, (dh) dorsal hood, (ty) typhlosole, (pa) palps, (he) heart, (am) adductor muscle, (rt) rectum, (in) intestine. **53.** Visceral ganglia. Scale bars = 1 cm.



Figures 54–61. *Saccostrea mordax*, shell and anatomical features. **54.** External view. **55.** Internal view of right valve; (ch) chomata, (im) muscle impression. **56.** Internal view of left valve, detail of undulations (pl) of the edge valves and umbonal cavity (uc). **57.** General view of soft part; (ho) hood, (an) anus. **58.** Mantle edge, detail of accessory heart (ah) and pallial muscles (pm); (ef) external fold, (mf) middle fold, (if) inner fold, (me) mantle edge. **59.** Detail of the palps (pa) and gills (gi). **60.** Heart; (ve) ventricle, (au) auricle. **61.** Visceral ganglia. Scale bars = 1 cm.



Figures 62–64. *Saccostrea mordax*, anatomical features. **62.** General view of soft parts; (pa) palps, (gi) gills, (vm) visceral mass, (he) heart, (rt) rectum, (an) anus, (am) adductor muscle, (pm) pallial muscles, (me) mantle edge. **63.** Stomach, right view; (pa) palps, (oe) esophagus, (sa) selection area, (gs) gastric shield, (dh) dorsal hood, (ty) typhlosole, (in) intestine. **64.** Visceral ganglia. Scale bars = 1 cm.

Saxostrea mordax.—Habe, 1951: 94; Kira, 1959: 127; 1962: 144; Taki, 1960: 192; Habe and Kosuge, 1966: 145; 1967: 137.

Saccostrea mordax.—Habe and Okutani, 1975: 194; Habe, 1977: 109; 1981: 83; Torigoe, 1981: 306, 328; Okutani and Soyama, 1987: 152; Habe and Matsuda, 1990: 98; Xu, 1997: 95; Hayami, 2000: 925.

Saccostrea cucullata—Morris, 1985: 125; Li and Qi, 1994: 170; Lamprell and Healy, 1998: 134 (*non* Born, 1778).

Description: SHELL: Shell elongated, to ~40 mm, with undulations on entire edge of both valves up to ligamentary region (Figure 54). Left valve concave, umbonal cavity well-developed, with extensive anterior projection (Figure 56). Right valve flat or slightly convex, not opercular (Figure 55). Color beige/cream, with edges of valves dark purple. Denticles present along edges; rounded, relatively large and distributed in single row (Figure 55). Adductor muscle scar oval, grayish or non-pigmented (Figure 55). MANTLE: Mantle thick, with pallial muscles more evident in adductor muscle region. Hood present, robust, filled by gonads and palps (Figure 57). Mantle edge thin, dark brown and yellow; middle fold with small and medium finger-like papillae; 2–4 small papillae for each larger one. Internal fold with small, uniformly distributed finger-like papillae. Accessory heart inverse-T shaped, well-marked, and surrounding ventral region of adductor muscle (Figures 58, 62). GILLS: Gills occupying ~½ of total area. Alimentary chamber narrow (Figures 59, 62). CIRCULATORY SYSTEM: Ventricle large, ~2/3 as large as auricles, with slight bundles more concentrated in posterior region; whitish. Auricles elongated, translucent (Figure 60). DIGESTIVE SYSTEM: Palps large and thick, ~½ of adductor muscle size, superior edge with folds; external palps covers ~1/3 of internal palps (Figures 59, 62). Esophagus long, twice as long as palps. Selection area of stomach (sa) long and narrow, ½ as high as esophagus; typhlosole in terminal region of globular portion (Figure 63). NERVOUS SYSTEM: Visceral ganglia with tree nerves in anterior and posterior region and one laterally (Figures 61, 64).

Type Material: Syntype, NMNH 5958 (examined).

Material Examined: CHINA: Taiwan, Taipei Co., Wanli, Yehliu, UF 303012, 3 specimens.

Distribution: Indo-West Pacific.

DISCUSSION

It is an accepted fact that the taxonomy of *Saccostrea* is problematic because of shell plasticity (Lam and Morton, 2006). Still, except for the shell, the anatomy of the species is mostly unknown (e.g., Lam and Morton, 2004, 2006, 2009). Among the species studied here, the only one with a described anatomy was *S. cucullata*, by Awati and Rai (1931).

The shell of *Saccostrea* differs from that of *Crassostrea* basically by the presence of chomata and the ornamentation of the edge in some species. Both genera have

medium to large-sized shells and occur in similar habitats, but *Saccostrea* species they were found only in the Pacific and Indian Oceans. An invasive species of the genus *Saccostrea*, found in São Sebastião (São Paulo, Brazil), is identified as *S. cucullata* (see Amaral and Simone, in press). As we demonstrate herein, among the *Saccostrea* species, taxonomy is problematic only when based solely on shell characters (even so, differences in shell morphology may be found when the characters are considered in sufficient detail). Anatomical characters are useful and sufficient for species-level identification. Methods in molecular systematics have been advocated as the only tools for identification of the various lineages of *Saccostrea* (Lam and Morton, 2006: 7). Observations of *S. mordax* suggest that it occurs only on exposed, wholly marine rocky shores, whereas other *Saccostrea* lineages occupy a wide range of habitats from brackish mangroves to somewhat less exposed marine shores (Lam and Morton, 2006).

Shell: The shells of *Saccostrea cucullata* are elongated, normally cup-shaped, with a deeply concave left valve showing an expansion in the ligament area. The right valve is flat or slightly convex, like a lid. The shell of *S. glomerata* is rounded, with a concave left valve slightly larger than the right valve, and a slightly convex right valve. In *S. echinata*, the shell is more elongated, with slight undulations, along the edge of the valves that stretch toward the central area. *S. palmula* has a rounded shell, with both valves laterally expanded; the left valve is larger than the right, and the right valve is small and opercular. *Saccostrea mordax* has a usually elongated shell, with undulations going from the margins to the ligament region; the left valve is concave, the right valve is almost flat or slightly convex, but it is not opercular as in the remaining species, and both valves have a similar width.

The shell edge undulations are characteristic of *Saccostrea*, with this character usually separating its species from those of *Crassostrea*. When present in *Crassostrea*, this undulation is only observed in the posterior region and in follicular layers.

The umbonal cavity is well-defined in *Saccostrea cucullata*, *S. echinata*, and *S. mordax*. In *S. glomerata* and *S. palmula* it is small or absent. According to Stenzel (1971: N995), the deepest umbonal cavities and the largest number of chambers are found in *Saccostrea*, particularly in the high-conical, rudist-like ecomorphs of the “living complex superspecies *S. cucullata*” from the tropical Indo-Pacific.

The shell edge in *S. cucullata* has small tubercles (elongated chomata). They are present along the inner edge of the right valve, with corresponding depressions on the left valve. In *S. glomerata*, the margins of both valves have well-developed angles; the right valve shows rounded chomata spread along its entire edge, arranged in single row, with corresponding depressions on the left valve. In *S. echinata*, the chomata are present along the right valve’s edge, with corresponding depressions on the left valve; these chomata are distributed in multiple rows

in the posterior region, and may have an elongated or rounded contour. *Saccostrea palmula* has evident projections and undulations along the shell's edge; following the pattern of expansions of the left valve, both valves show more rounded chomata on the edge than those of *S. cucullata*, which is restricted to the anterior region, aligned and uniformly distributed. The corresponding depressions on the right valve are somewhat shallow. *Saccostrea mordax* has chomata along the edges on both valves; they are rounded, relatively large and distributed in a single row.

Some oysters have chomata distributed around the peripheries of their valves, including the valve margins directly opposed to the hinge. True teeth are never found in this area of bivalve shells. Chomata are not analogous to teeth or sockets. The genus *Saccostrea* has strongly developed chomata, tall and strong tubercles on the right, and deep pits on the left valves along the whole periphery of the valves (Stenzel, 1971).

In *Saccostrea cucullata*, the external surface of the valves is variable in color, from pale white, light-gray to dark-brown, greenish, or purple. The internal surface is white, and may present purple spots. These characteristics support those presented by Awati and Rai (1931). *Saccostrea glomerata* is internally colored dark brown at the edges, fading toward the median region of the shell. Comparatively, *S. echinata* is colored white/cream to grayish. *Saccostrea palmula* is colored white/cream with purple spots externally, and the internal surface is white and slightly nacreous; there may be purple spots in the region corresponding to the mantle edge on both valves. In *Saccostrea mordax*, color is cream in the middle, with dark purple colored in the internal margins.

The adductor muscle scar in *Saccostrea cucullata* is reniform, striated, white or grayish. In *S. glomerata*, the adductor muscle scar is reniform, occupying 1/5 of total area, located in the median region, with anterior portion normally pigmented gray/brown and a posterior portion with pigmented lines. Its surface is slightly opalescent and white. In *S. echinata*, the adductor muscle scar is also reniform but more elongated and unpigmented; in *S. palmula*, it differs from the above-mentioned species: the adductor muscle scar is defined by concentric purple lines in the anteroventral portion of the valves, but it is also reniform. *S. mordax* has an oval adductor muscle scar, grayish, with concentric lines that may be pigmented. These characteristics fit with those described by Lam and Morton (2009).

All species of *Saccostrea* exhibit a slight Quenstedt muscle scar, a rounded mark located in the anteroventral region of the valves. These imprints have been noticed on many oyster species, fossil and living (Dall, 1880; Hedman and Boyce, 1890; Stenzel, 1971; Harry, 1985).

The adductor muscle (and scar) of Crassostreinae in general do not differ among genera but show variations among species. These variations have been pointed out in the literature (Nascimento, 1991 for *C. rhizophorae*; Galtsoff, 1964 and Kennedy et al., 1996 for *C. virginica*),

and are possibly associated with the high level of shell plasticity.

Adductor Muscle: The adductor muscle is short and stout and directly connects the two valves. It is differentiated by its whole length into two coalescent subdivisions: the catch muscle (with opalescent and opaque color in live oysters, comprising the ventral or distal part of the muscle), and the quick muscle (flesh, colored and translucent, comprising the dorsal or proximal part of the muscle). The relative sizes of the two subdivisions differ among genera (Stenzel, 1971). *Ostrea* has a larger catch muscle than *Crassostrea* and *Saccostrea*; *Hytissa* has the smallest one.

Saccostrea cucullata shows a normally reniform adductor muscle, which is sometimes oval while *S. palmula* has a strictly reniform muscle. *Saccostrea glomerata* has a reniform adductor muscle, with a convexity in the posterior region. *Saccostrea echinata* also has a reniform adductor muscle, but with a convexity toward the posterior region (that of *S. cucullata* is anterior). *Saccostrea mordax* has a strictly oval adductor muscle.

The Quenstedt muscles are a pair of tiny muscles, each attached at one extremity to a valve, and having the opposite extremity ending among the oral part of the gills. The pair of Quenstedt muscles has no differentiation regarding the origin on the shell and the insertion in the base of the palps in the five species. Galtsoff (1964), Stenzel (1971), and Mesquita (1993), observed that the Quenstedt muscles are difficult to find, but, according to Amaral and Simone (2014), the pair of Quenstedt muscles are visible when opening the valves in all species of Crassostreinae. From their origin on the shell, the muscles run through the anterior visceral mass up to the insertion in the base of the palps. This peculiar morphological arrangement shows no probable homology with the anterior adductor muscle or any foot muscles (Galtsoff, 1964; Stenzel, 1971).

Mantle: The mantle lobes of an adult oyster are thick and somewhat solid, having many muscle strands, some arranged in concentric and others in radial patterns (Stenzel, 1971). In *Saccostrea cucullata*, the lobes are thick, with well-defined pallial muscles, mainly around the adductor muscle; the hood is robust, well-defined, normally free or filled by gonads. In *S. glomerata*, the mantle is slightly thick, with pallial muscles more evident in the adductor muscle region, and the hood is absent. In *S. echinata*, the mantle lobes are thin, with well-defined pallial muscles along the mantle's extension. It has a smaller hood than *S. cucullata*. *Saccostrea palmula* has a thick mantle with pallial muscles more evident around the adductor muscle. The hood is not present. In *S. mordax*, the mantle lobes are thick with pallial muscles more evident in the adductor muscle region. It also has a well-defined hood, filled by gonads and palps. The pallial muscles show some differences among species, in quantity, girth, or location.

Saccostrea cucullata has a thick mantle edge, colored dark yellow with brown spots. Its three folds have similar size; the middle and inner folds also have finger-like papillae, one or two short for each long one. *Saccostrea glomerata* has a thick mantle edge with reddish color; the middle fold has both short and long papillae, at a ratio of three to four short for each long one; the inner fold has short and medium papillae, usually two or three medium for each short one. In *S. echinata*, the mantle edge is thick and colored yellow and/or brown; the papillae of the middle fold are alternately long and short, with three short for each long one. *Saccostrea palmula* has a thin edge, colored beige/cream; the finger-like papillae of the middle fold are small, elongated, alternately short and medium/long. Usually, two to five small papillae are present for each one or two long/medium ones. *S. mordax* has a thin edge, colored dark brown and/or yellow; the middle fold bears medium and short finger-like papillae, at a ratio of two to four short papillae for each medium one; the internal fold bears small, uniformly distributed finger-like papillae. This variation (size and distribution) was also found in Amaral and Simone (2014) for *Crassostrea* species.

The accessory heart in *Saccostrea cucullata* has three well-defined branches in the right lobe, forming a short y-shaped structure while the left lobe shows only a single large branch. In *S. echinata*, the accessory heart is slim, translucent, with thin walls, not reaching the adductor muscle in both lobes. In *S. palmula*, it has tree branches that contour the adductor muscle. *Saccostrea mordax* shows a different arrangement, forming a well-defined inverted T-shaped structure, and girdling the adductor muscle in the ventral region. *Saccostrea glomerata* has three branches in both lobes, forming a thick y-shaped structure, and one branch, about 1/3 thinner, which borders the adductor muscle.

Differently from the species described here, *Crassostrea* had tree branches in all studied species in Amaral and Simone (2014). This characteristic can be used as a distinction between *Saccostrea* and *Crassostrea*.

The promial passage was first reported by Kellogg (1892: 396–397). Nelson (1938) was the first to recognize its significance and to elucidate its function. The promial passage is present in all *Saccostrea*. This is a characteristic of the nonincubatory ostreid genera (e.g., *Crassostrea*, *Saccostrea*, *Striostrea*, *Hyotissa*, *Neopcyndonte*; Stenzel, 1971). The promial passage varies in size: in species of *Crassostrea* it appears on both sides as a long chamber, from the margin of the visceral mass to the base of the gills; in *Saccostrea*, the passage is open only in the left lobe and open to half of length of the visceral mass.

Gills: The number of gill folds and filaments is very variable, apparently increasing proportionally to the animal's size. However, these numbers can vary among individuals of similar size. Ridewood (1903) mentioned 9–12 filaments per fold in *Ostrea edulis*, while Atkins (1937a) mentioned 8–17. Atkins (1937a) mentioned 8–17 in *Crassostrea virginica*; Nelson (1938) mentioned 8–15. Galtsoff (1964) mentioned 10–16 filaments per fold in

C. angulata, while Atkins (1937a) referred to 15–16 and Nelson (1938) 8–14 filaments per fold. Amaral and Simone (2014) observed that the number of filaments per fold in *C. rhizophorae*, *C. mangle*, *C. brasiliiana*, and *C. virginica* varies from 12 to 13, reaching 15 in *C. gigas*. Based on the similarity of these numbers, this parameter seems to be of little use in distinguishing the examined species. In all species of *Saccostrea* studied here, the variation is of 12–14 filaments per fold. The gills of all species in this study occupy about 1/2 of the pallial cavity area. *Saccostrea cucullata* has a medium-sized alimentary chamber, approximately 1/3 as thick as the gill fold; *S. echinata* has a thick chamber, about 1/2 as thick as the fold; *S. palmula*, *S. mordax*, and *S. glomerata* have narrow alimentary chambers, about 1/5 as thick as the gill fold.

Visceral Mass: An oyster is composed of two major interconnected subdivisions: 1) visceral mass, containing all the organ systems (digestive, excretory, reproductive), most of the muscles, and much of the nervous and circulatory systems; 2) gills and mantle/shell, which is composed of a hard portion (shell) that protects all other organs and soft parts, the mantle, which carries sensitive organs, as well as lesser parts of musculature, nervous and circulatory systems (Stenzel, 1971).

The visceral mass extends from the ventral region of the ligament to the anterior surface of the adductor muscle. It is formed by normally yellowish-colored gonads, with abundant digestive diverticula and renopericardial structures, and occupies nearly 1/4 of the total body size in all species. The gonads of all species are massive, apparently regardless of the gonadal maturation period, and surround the whole visceral mass, in some cases surrounding the region near the pyloric process. They are usually colored beige or yellowish. The genital opening has been observed in *S. cucullata* in the kidney and distinguishes itself from the surrounding area by a brownish spot.

Pericardium/Heart: The heart is located in the pericardium, a thin-walled chamber between the visceral mass and the adductor muscle. On the right side, the promial chamber extends down over the heart region and the mantle separates the pericardium wall from the shell (Galtsoff, 1964). In most Lamellibranchia, the rectum perforates the heart and passes through it, but in *Ostrea*, the heart and rectum remain apart, the heart lying beneath the rectum (Awati and Rai, 1931).

Saccostrea cucullata has a slightly enlarged ventricle with thick walls, of opaque-white color; the auricles are thin-walled and translucent and bear external sac-like structures. *Saccostrea glomerata* has a robust heart, with a relatively large ventricle, colored light cream; the auricles are elongated, robust and have the same color as the ventricle. *Saccostrea echinata* has a thin ventricle, normally translucent, and two non-pigmented auricles, both more elongated than in *S. cucullata*. The ventricle is elongated in *S. palmula*, slightly thick and whitish; the auricles are small and non-pigmented. *Saccostrea mordax* has a large ventricle, about 2/3 the size of the auricles, with whitish

coloration; the auricles are translucent and elongated. The heart size and coloration are variable in Crassostreinae.

Palps: The outline of the palps is hatchet-shaped and slightly different in each genus (Stenzel, 1971). The labial palps are large triangular flaps lying in front of the gills and attached to the visceral mass by the broad base (Awati and Rai, 1931). The palps of *Saccostrea cucullata* are large, spatuliform, have a folded anterior edge and a slightly arched ventral region. In *S. glomerata*, the palps occupy $\sim 1/5$ of the visceral mass area and are also spatuliform; their internal surface bear plicae that extend transversely to the edge. The palps of *S. echinata* are small, arched, sickle-shaped, with folds along the anterior margin. The external palps are fused in the middle, overlying the inner palps. In *S. palmula*, the palps are larger than those of the remaining species, thin, with a superior margin bearing folds. *Saccostrea mordax* has large and thick palps, with folds in the superior margin, as is the case in *S. echinata*, and the external palps overlie the inner palps for about $1/3$ of their length.

Esophagus: The mouth leads into a long esophagus; the esophagus lumen is dorsoventrally compressed and appears as a narrow slit in transverse sections. The lumen becomes narrower as it passes backward and upward to enter the dorsal region of the stomach (Awati and Rai, 1931). The esophagus is dorsoventrally compressed in all the study species; in *Saccostrea cucullata*, it is short and large, $1/2$ of palps in size; in *S. glomerata*, it is long and narrow, and also $\sim 1/2$ of palps size. In *S. echinata*, it is long and thin, and $\sim 1/3$ as long as the palps; in *S. palmula*, it is elongated and thin, and $\sim 2/3$ of palps size; in *S. mordax*, it is large and long, of same size as the palps.

Stomach: The stomach is a large sac occupying a central position in the visceral mass. This is true also for *O. edulis* (Yonge, 1926; Graham, 1949; Purchon, 1957; Reid, 1965), *C. parasitica* (Shaw and Battle, 1957) and *O. chilensis* (Purchon, 1957). Other details of the morphology and physiology of the digestive tract in Ostreidae, such as ciliary mechanisms and stomach structure and operation, can be found in the literature (Shaw and Battle, 1957; Nelson, 1960; Reid, 1965; Yonge, 1966). Internally, the study species differ in the selection area 1 (sa1), typhlosole, gastric shield, and dorsal hood. The sa1 in *Saccostrea cucullata* is short and large, with the typhlosole beginning in the posterior region of the stomach; *S. echinata* has a longer sa1, and the typhlosole begins more posteriorly than in *S. cucullata*. In *S. palmula*, the sa1 is short and narrow, with the typhlosole beginning laterally. The sa1 in *S. mordax* is long and narrow and the typhlosole is located more posteriorly than in *S. cucullata*.

The stomach has been described as bag-shaped, internally divided into a smaller anterior chamber and other larger posterior chamber, by means of a thick fold; such a fold is projected to the organ's lumen and seems to serve as a means to direct particles to the posterior region through a narrow channel (Shaw and Battle, 1957). The dorsal

hood length is nearly $1/2$ of the length of the sa1 in *S. cucullata*. In *S. mordax*, the dorsal hood has about the same length as the sa1. In *S. echinata* and *S. palmula*, the dorsal hood is short and narrow, about $1/2$ the size of those of other species.

Intestine, Rectum, Anus: The mid-gut, or intestine, originates from the stomach on the right side of the style-sac, turns around immediately to its left, and runs parallel to it all along its length; on reaching the distal end of the style-sac, the intestine turns anteriorly and runs completely back on this course (Awati and Rai, 1931). The intestine, before the style sac, passes behind the pericardium, immersed in the gonads in the visceral mass. In *Saccostrea cucullata*, *S. echinata*, *S. mordax*, and *S. glomerata*, the intestine passes behind the pericardium; in *S. palmula*, behind the esophagus. The rectum of *S. cucullata* is long and thin, surrounding the adductor muscle in $2/3$ of its concave region, with the anus bearing a single fold. *Saccostrea echinata* has a larger elongated rectum, with a shell-like anal expansion; *S. palmula* it is short and large, with the anus ending in a bell-shaped fold. *Saccostrea mordax* has a short and large rectum, and the anus bears a single fold.

In all living oysters, except for the Pycnodontinae, the rectum skirts the dorsal flank of the pericardium. In the Pycnodontinae, the rectum passes through the pericardium and the ventricle of the heart, and the anal papilla is more projected. These relative positions of the rectum and ventricle in oysters are of great taxonomic importance.

Central Nervous System: The nervous system is relatively simple, showing a pair of cerebral ganglia and a pair of visceral ganglia connected by commissures. The cerebral ganglia are somewhat inconspicuous because of their very small size and location in the visceral mass. The visceral ganglia can be easily distinguished in the anterolateral region of the adductor muscle. *Saccostrea cucullata* and *S. glomerata* have two pairs of nerves in the anterior region and three in the posterior region; *S. echinata* presents two pairs in the anterior and posterior regions; *S. mordax* and *S. palmula* have three pairs in the anterior and posterior regions.

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